

# Trophic heterogeneity in salt marshes of the northern Gulf of Mexico

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**ABSTRACT:** Predator-prey interactions in salt-marsh ecosystems are driven primarily by interactions among tidal dynamics, local physiography, and macrophyte density. Distinct seaward-to-landward predation gradients have been described for the continuous and expansive meadows of *Spartina alterniflora* on the Atlantic coast of the United States. In the northern Gulf of Mexico, *Juncus roemerianus* dominates and *Spartina* is generally limited to fringing bands or disjunct patches in low-lying areas. It is not known whether predation regimes vary consistently among subhabitats in these disjunct marshes. We investigated whether small-scale variations in topography and habitat structure produce persistently distinguishable predation regimes among marsh patches in coastal Alabama. Each of our study sites was representative of the principal subhabitats found within continuous *Spartina* meadows: vegetation bordering open water, tidal creeks within the marsh, and interior subhabitat. We assessed a strong trophic interaction in these subhabitats: predation pressure exerted by the blue crab *Callinectes sapidus* on the periwinkle *Littoraria irrorata*. The distribution of sublethal repairs in *Littoraria* shells demonstrated that attacks by *Callinectes* were randomly inflicted, irrespective of attack frequency. The occurrence of sublethal shell repair was positively related to the frequency of predatory attacks on experimentally tethered snails, the abundance of crabs, and the degree of antipredatory architectural defense in the snail shells. Among-site differences in shell repair and architectural defense were related to topography and habitat structure, and these differences persisted over multiple seasons and years. Physical variations thus maintain strong, persistent predation regimes among subhabitats in disjunct *Spartina* marshes.

**KEY WORDS:** *Callinectes sapidus* · *Littoraria irrorata* · *Spartina alterniflora* · Predation · Salt marsh · Sublethal shell damage · Tethering experiment

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## INTRODUCTION

The significance of predation in structuring marine communities is heavily influenced by physical and biological gradients at a variety of scales and hierarchical levels. Vertical gradients in predation pressure are generally established along rocky shores by wave action, competition, and the threat of desiccation, resulting in high levels of predation in the subtidal zone and decreasing predation intensity as one moves up into the intertidal (e.g. Paine 1974, Menge 1976). Wave action can also establish horizontal gradients in the rocky intertidal, as evidenced by the presence of larger and better-defended prey on protected shores relative to

conspecifics on wave-exposed shores (Menge 1978a,b, Trussell 1996, Boulding et al. 1999). Within the subtidal zone, the structural complexity generated by hard-bottom environments such as reefs and other topographic features (Connell & Jones 1991, Wahle & Steneck 1991), and vegetated habitats such as seagrass meadows (Hovel & Lipcius 2002, Hovel & Fonseca 2005), kelp forests (Carr 1994, Anderson 2001), and drift algae (Adams et al. 2004), affords refuge to prey. Furthermore, the patchy nature of these habitats generates fine-scale variations in accessibility to predators through the formation of interior and edge subhabitats.

Habitat fragmentation—the reduction of continuous areas of habitat to small, disjunct patches—can

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strongly influence the biotic interactions that structure communities (e.g. Forman & Godron 1986, Kareiva 1987, Robinson et al. 1995). Although habitat fragmentation studies have been largely restricted to terrestrial environments, the effects of fragmentation in marine habitats such as seagrass meadows (Bologna & Heck 2000, Hovel & Lipcius 2001), kelp forests (Dayton & Tegner 1984), and coral and oyster reefs (Eggleston et al. 1998) have received increased attention over the past decade. Predation intensity is often positively correlated with increased edge habitat and decreased patch size and, as these studies illustrate, can significantly alter prey survival, community structure, and species diversity.

The interactions between physical and biological factors are particularly complex in intertidal salt-marsh habitats. Predator-prey interactions within salt marshes are ultimately driven by the overarching influence of tidal dynamics and their interaction with local topography. By dictating the duration of flooding, tides shape the vertical and horizontal distribution of organisms and vegetation, the potential duration of predator-prey encounters, and variations in structural complexity conferred by marsh vegetation (Wiegert & Pomeroy 1981, Kneib 1984, West & Williams 1986, Bertness & Ellison 1987). The foraging environment available to aquatic predators shrinks and expands with the tides, becoming more hostile to aquatic organisms with increasing distance landward from the water's edge. Along the Gulf and Atlantic coasts of North America, the smooth cordgrass *Spartina alterniflora* (hereafter *Spartina*) is the dominant macrophyte below mean high water and occurs in 2 distinct growth forms: tall- and short-form. Tall-form *Spartina* generally borders open water and is characterized by low grass densities, whereas dense swards of short-form *Spartina* are found in the poorly drained soils of the high marsh (this study, Weigert & Pomeroy 1981, West & Williams 1986, Silliman & Bertness 2002). Increased grass densities, coupled with the topographical controls discussed above, can impose a filter on both the size and number of predators capable of reaching the inland regions of the marsh (West & Williams 1986, Schindler et al. 1994, Lewis & Eby 2002).

Measures of biomass, abundance and species diversity are typically used as proxies for the activity, resource availability and resource utilization of mobile invertebrates and fish among subhabitats (i.e. edge and interior zones) in *Spartina* salt marshes (Kneib & Wagner 1994, Peterson & Turner 1994, Whaley & Minello 2002). These 'snapshot' studies illustrate the importance of habitat heterogeneity for maintaining diversity and sustaining secondary production within salt marshes. They are, however, poor methods for capturing the variability of biotic interactions.

Those studies that described distinct seaward-to-landward predation gradients using dynamical measures in salt marshes were conducted almost exclusively in the *Spartina*-dominated, coastal Atlantic marshes in the eastern United States, where a large tidal range facilitates the formation of expansive *Spartina* meadows (Lin 1989, 1990, Schindler et al. 1994, Lewis & Eby 2002, Silliman & Bertness 2002). The characteristic scales of biotic gradients are less well understood for marshes in the northern Gulf of Mexico. With the exception of the Mississippi River delta, these marshes are typically disjunct and, due to the narrow tidal range (0.4 to 0.6 m), limited to low alluvial deposits (Stout 1984, Mitsch & Gosselink 1993). As a consequence of these characteristics, Gulf marshes are dominated by *Juncus roemerianus*, and *Spartina* is generally limited to fringing bands or disjunct patches in low-lying areas. Earlier attempts to measure the distribution of predation regimes (i.e. spatial variations in the intensity of predatory-prey interactions) in Gulf *Spartina* marshes were limited in their spatial extent (West & Williams 1986). It remains unclear whether predation gradients observed thus far on either the Atlantic or Gulf Coasts reflect typical predator-prey dynamics within the patchwork of disjunct *Spartina* marshes that characterizes the northern Gulf of Mexico. More specifically, are predation regimes relatively homogenous among patches, owing to their small spatial extent and proximity to open water, or do small-scale variations in topography produce persistently distinguishable predation regimes?

This study had 2 primary goals. The first was to determine whether variations in predation intensity of the blue crab *Callinectes sapidus* on the marsh periwinkle *Littoraria irrorata* (hereafter *Callinectes* and *Littoraria*) within small, disjunct patches of *Spartina* represent points along a seaward-to-landward continuum of predation intensity (i.e. individually represent distinct subhabitats) observed in continuous *Spartina* meadows. This was accomplished via tethering experiments and assessments of sublethal repair and architectural defenses in the shells of *Littoraria*. The second goal was to characterize the temporal and spatial variability of predatory interactions in an effort to determine the extent to which predation regimes vary on a multi-year time scale. An additional outcome of the study was our discovery of a rapid and inexpensive method for assessing habitat and resource use by *Callinectes* in natural and restored *Spartina* salt marshes.

## STUDY SPECIES AND SITES

**Focal species.** *Callinectes* is an abundant and highly mobile predator within *Spartina* marshes. This species is a generalist: its diet consists primarily of fish, mol-

lusks, crustaceans, infauna, and plant detritus (Laughlin 1982, Fitz & Wiegert 1991, Hsueh et al. 1992). Although *Littoraria* comprises only a portion of the diet of *Callinectes*, the crabs are the primary predators of post-metamorphic snails (Hamilton 1976, Warren 1985). *Littoraria* is an abundant supratidal herbivore that grazes fungi from dead and senescing *Spartina* plants. It has been implicated in facilitating the senescence of *Spartina* leaves through the process of fungal farming (Silliman & Newell 2003) and, by controlling populations of *Littoraria*, *Callinectes* potentially plays a role in preventing the snails from overgrazing *Spartina* (Silliman & Bertness 2002).

*Littoraria* migrate upward along *Spartina* plants on the incoming tide. Although vertical migration does decrease mortality by *Callinectes* (Warren 1985), previous studies indicate that the migration is closely linked to the tidal cycle and other environmental cues rather than to water-borne predatory cues produced by *Callinectes* (McBride et al. 1989, Henry et al. 1993, Hovel et al. 2001). Despite the snails' climbing efforts, *Callinectes* often swim to the water's surface or climb the plants to knock *Littoraria* into the water, where the crabs attack them (Hamilton 1976). Each attack results in 1 of 3 possible outcomes: the shell is crushed and the snail is consumed, the snail is released undamaged, or the snail escapes in a damaged condition. Sublethal damage is generally restricted to the leading edge of the outer whorl of the shell, which is subsequently repaired by the snail's mantle and is preserved as a scar.

**Study sites.** Our study sites represent the principal subhabitats present in continuous *Spartina* meadows in the northern central Gulf of Mexico and vary in their potential accessibility to *Callinectes*. We chose 2 salt-marsh locations in Alabama for our experimental work: Airport Marsh, Dauphin Island and Point-Aux-Pins, Bayou La Batre. These sites are located along the southern and northern shores of Mississippi Sound, respectively (Fig. 1). *Littoraria* shell fragments are abundant in salt marshes throughout Alabama and Mississippi, underscoring the importance of shell-crushing predation as a significant source of mortality. Within each of our study marshes, we established two 100 m<sup>2</sup> sites within probable high- and low-predation microhabitats based on their accessibility to *Callinectes*.

A site located on the northern shore of Airport Marsh, APM1, consists of a large depression inhabited exclusively by *Spartina*. The site is isolated from open water by a low, 3 m wide, vegetated berm. Access by crabs to the depression is restricted to a narrow tidal creek that connects directly to Mississippi Sound. A second site, APM2, is isolated from APM1 by a road. It is located within the interior of a high-marsh zone

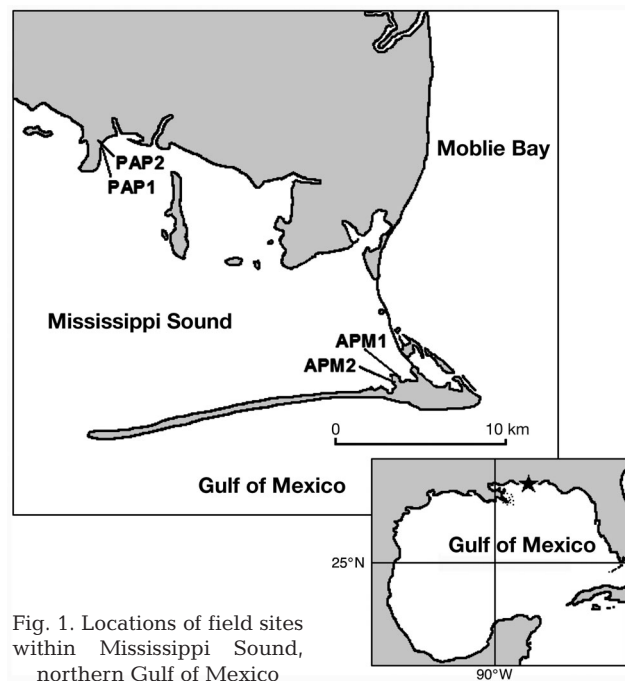


Fig. 1. Locations of field sites within Mississippi Sound, northern Gulf of Mexico

dominated by short-form *Spartina* and moderately dissected by tidal creeks. APM2 is located approximately 30 m from the nearest tidal creek (i.e. the most isolated configuration available). At Point-Aux-Pins, PAP1 is located along the shore within a continuous, 8 m wide band of tall-form *Spartina*. PAP2 encompasses a small tidal creek (~15 m long) that drains into a wide, shallow secondary tidal channel. The period of marsh inundation is similar at PAP2, APM1, and APM2 (3 to 6 h per day), and is highest at PAP1 (almost constantly inundated with the exception of the lowest of spring tides). Both APM1 and PAP2 constitute distinct patches of *Spartina*, intermediate in height between PAP1 and APM2, which grade into *Juncus roemerianus* and other upland vegetation.

Within our *a priori* hypothesis of a predation 'gradient', we designated APM2 (located within an interior region of the marsh) and PAP1 (located in edge habitat) as endpoints of low and high predation intensity, respectively. APM1 and PAP2 were expected to fall between these extremes. These sites represent disjunct marsh subhabitats; therefore, this study does not address within-marsh gradients per se (i.e. within-site variability).

**Other potential predators of *Littoraria*.** The crown conch *Melongena corona* and other predatory gastropods, common in seagrass and adjacent salt-marsh meadows in subtropical ecosystems, are not present in salt marshes of the northern Gulf of Mexico west of the mouth of Mobile Bay and, therefore, are not found within our study area. Birds, and the clapper rail *Rallus*

*longirostris* in particular (Heard 1982), are potential sources of predation on *Littoraria*, but the magnitude of their impact on snail populations is not known. However, previous caging experiments in northwestern Florida suggest that birds are not significant predators of *Littoraria* (Warren 1985). Herons, egrets, and rails were frequently observed to forage during periods of low water at APM2 and in tidal pools adjacent to APM1 and PAP2 (foraging birds were rarely observed within the sites themselves). Birds were not observed foraging at PAP1 during the course of the study; the absence of birds at this site is attributed to relatively strong wave action and frequent tidal inundation.

Xanthid mud crabs (*Panopeus herbstii* and *Eurytium limosum*) and their burrows were observed at APM2, APM1, and PAP2, but not at PAP1. Although we did not quantify burrows in this study, crab counts from baited traps yielded an order of magnitude more *Callinectes* than xanthids. These results suggest that *Callinectes* is the dominant predator of *Littoraria* within our sites (see 'Results'). Xanthid burrows were limited to creek banks within both marshes, and were present in far fewer numbers than those reported by Silliman et al. (2004) from the Atlantic coast.

## MATERIALS AND METHODS

**Sampling schedule.** The bulk of this study was conducted from April to November 2003, the time of year during which activity of *Callinectes* is maximal in the salt marshes of Alabama (West & Williams 1986). This time frame was divided into 3 equal intervals, defined as spring, summer and fall. *Callinectes* activity is limited during the winter months because the crabs migrate to deeper water or offshore habitats. Additional measurements were made in 2001 and 2002 and are described below.

**Predation potential.** We measured predation potential using tethering experiments. Despite objections to the use of tethering experiments (Peterson & Black 1994, Kneib & Scheele 2000), the approach is useful for comparing predation potential (defined by Aronson [1987, 1989] as the activity of predators) among sites that contain the same suites of predators (Aronson & Heck 1995, Aronson et al. 2001). Potential sources of predation other than *Callinectes* increase as one moves into the high marsh (see 'Other potential predators of *Littoraria*' above). The effects of these additional sources of predation should compensate differences in the magnitude of predation intensity by *Callinectes* across subhabitats. Thus, if other predators exert significant predation pressure on *Littoraria*, the bias is in the opposite direction of our hypothesized 'gradient' of *Callinectes* activity, and therefore provides a conservative test.

*Littoraria* of 14.5 to 16.5 mm shell length (the smallest size range consistently available throughout the year) were affixed to 5 cm lengths of polyethylene line by a loop around the junction of the body whorl and the penultimate whorl using cyanoacrylate adhesive. Snails were individually tethered to shoots of *Spartina* at each study site. The short length of the tethers prevented the snails from exiting the water during high tide, but permitted grazing on the substratum. Although the use of long tethers would permit snails to migrate with the tides and provide more 'natural' estimates of attack rates, longer lines are more prone to tangling and could lead to tethering artifacts.

The polyethylene line resisted shearing forces imposed by the predatory activities of crabs. This reduced the loss of snails as a result of severed tethers. Crimps and frays in the lines enabled us to determine if an attack had occurred even if the snail had disappeared from the tether. In the laboratory, handling of tethered snails by *Callinectes* always resulted in crimps and frays in the line within 3 to 5 mm of the knot used to secure the line to the spire of the snails ( $n = 20$  tethered snails; 3 snails were rejected outright with no damage to the line or shell). Mud crabs that handled tethered snails did not produce marks on the lines ( $n = 15$  tethered snails). Damage of this sort to the line was not observed in caged controls in the field.

In each trial, we tied single tethers to the bases of 15 randomly selected *Spartina* shoots within the 100 m<sup>2</sup> study plot at each site (10 snails were used for 2 fall trials). We conducted 5 replicate tethering trials at each site over 5 randomly chosen 24 h periods per season. Tethers were deployed either simultaneously at all sites (i.e. during the same tidal cycle) or over consecutive tidal cycles at all marsh locations, in order to ensure equivalent tidal conditions for each trial. After 24 h, which essentially corresponds to a single tidal cycle in coastal Alabama, the tethers were collected and the proportion of attacked snails was assessed for each site. A predation event was scored if the snail or its tether met one or more of the following criteria: (1) the entire shell was crushed; (2) the shell was intact but the lip was damaged; (3) the shell was absent or undamaged but the tether was crimped or frayed. Empty shells were only recovered from 5 tethers, were not specific to any one site, and were excluded from analysis.

Controls consisted of 10 individually caged snails tethered to individual *Spartina* shoots and were set simultaneously with alternating tethering trials. All controls were placed at PAP1, the site that exhibited the greatest wave energy. Cages measured 20 cm on each side and were secured to the substrate with steel stakes. We tested whether hydrodynamic conditions differed for caged and free snails by measuring the

dissolution rates of plaster blocks set within and outside the cages for 24 h. No significant differences were detected between the dissolution rates of the caged and non-caged plaster blocks (*t*-test;  $n = 10$  blocks for both caged and non-caged treatments;  $p = 0.114$ ).

The proportions of attacked snails were divided into 3 assessment classes: (1) lethal attacks; (2) sublethal attacks; (3) cases of predator-specific line damage (crimps and frays close to the knot). The total number of predation events was calculated as the sum of classes 1, 2 and 3. This was done to detect predation regimes produced by predators other than *Callinectes*. For example, the presence of a highly effective predator in the high marsh could enhance the number of crushed snails without leaving signs of sublethal damage or damage to the tethers. Each class of predation and totals were analyzed separately using a 3-way ANOVA design, with site (APM1, APM2, PAP1, and PAP2) and season (spring, summer, and fall) defined as fixed factors and the day of the tethering trial nested within season. Tukey multiple comparisons tests were performed where appropriate. Bartlett's test was used to analyze homogeneity of variances, and normality was examined using the Anderson-Darling test, for this and all other analyses. The tethering data did not require transformation because they met the assumptions of parametric statistics.

**Test for statistical independence among tethering trials.** Although *Callinectes* is not known to exhibit homing behavior in intertidal habitats (reported by Fitz & Wiegert [1991] based on their observations from Sapelo Island, Georgia), crabs were trapped, tagged and released to ensure independence among our replicate tethering trials. Traps were deployed for 24 h once per week for a total sampling period of 6 wk at APM1 and APM2 in September and October, 2002. Juvenile crabs <50 mm in carapace width were given a unique identifying mark with permanent ink, and those >50 mm carapace width were implanted with numbered tags (Floy T-bar anchor tags). These collections constituted a separate study from those that measured predator abundance and size.

**Sublethal damage.** To compare levels of sublethal damage among sites and seasons, living snails from each of 3 size classes (small: 5.00–11.99 mm; medium: 12.00–16.99 mm; large:  $\geq 17.00$  mm) were randomly collected from each site once per season in 2003. Due to seasonal variability in snail recruitment and the size structure of snail populations among sites, sample sizes were 30 to 57 for large snails, and 30 to 50 for medium snails. Sample sizes for small snails ranged between 25 and 50, with the exception of a collection of 87 snails at PAP1 during spring and 16 snails at PAP2 during fall. Small snails were not consistently available throughout the year at APM2, and that site was excluded from analysis.

In a separate analysis, we compared levels of repair in large snails collected during the fall of 2001, 2002, and 2003 to test whether repair in large snails remained constant from year to year. We collected 50 snails at each site during October of each year with the exception of PAP2 in 2003 ( $n = 30$ ). All snails were collected during low tide.

Prior to examination, all shells were cleaned with a wire brush to ensure that repairs on the spire were not obscured by epibionts or debris. Repairs were counted on all whorls of the shell with the aid of a dissecting microscope. These repairs were interpreted relative to reference collections obtained from snails damaged by *Callinectes* in aquaria. To avoid biases in repair frequency associated with erosion of the early whorls (e.g. Stanhope et al. 1982), snails were randomly collected in bulk; only those individuals, randomly drawn from the bulk sample, on which the spiral cords (raised ridges on the surface of the shell oriented in the direction of shell coiling) were clearly visible over the entirety of the body whorl and penultimate whorl were included in our assessments of repair.

Expressing sublethal damage as the proportion of snails in an assemblage bearing one or more repairs (henceforth 'proportion of repair') potentially underestimates predation intensity if individuals bear multiple repairs (Kowalewski et al. 1997, Alexander & Dietl 2003). On the other hand, expressing damage as the mean number of repairs per snail (henceforth 'frequency of repair') could overestimate predation intensity if sublethal injuries predispose the snails to subsequent attacks (Aronson 1989). However, if repairs are randomly distributed within a population, the 2 methods of assessing sublethal damage should provide equivalent, unbiased information. We assessed repair using both metrics and tested the statistical distribution of repairs within each site.

If the number of snails in an assemblage with [ $N, N+1, N+2, \dots, N+x$ ] scars are randomly distributed in an assemblage, one can infer that scarred snails are not prone to incurring more or fewer future scars. This would imply both that recently damaged snails do not alter their behavior after an attack, and that sublethal attacks are randomly inflicted by predators. If repairs are not randomly distributed, it is possible that snails alter their behavior after a sublethal attack, and/or that particular individuals are preferentially attacked by predators.

For each sample of snails (i.e. for every combination of site, season, size class, and year), we tested whether repairs were randomly distributed among snails. The frequency distributions of repairs were compared to Poisson distributions using  $\chi^2$  goodness-of-fit tests. A Bonferroni correction was applied to the individual tests to maintain an experiment-wise error rate of  $\alpha = 0.05$ .

We made comparisons among sites and seasons, and sites and years, using both metrics of sublethal repair discussed above. We performed mutual tests of independence for proportions of repaired snails among sites, seasons, and repair presence/absence using  $4 \times 3 \times 2$   $\chi^2$  contingency tables (Zar 1999). We tested the 3 size classes separately. Partial tests of independence were then performed to determine which factors were not independent of the others. For size classes in which no significant differences were detected among seasons, the data were pooled across seasons within each site and pair-wise differences in repair presence/absence between sites were examined using  $2 \times 2$  contingency tables.

We also used  $4 \times 3 \times 2$   $\chi^2$  contingency tables to test for independence among sites, years, and repair presence/absence. Partial tests of independence and  $2 \times 2$  contingency tables were applied as needed. Bonferroni corrections were calculated separately for the  $4 \times 3 \times 2$  and  $2 \times 2$  contingency tests, and applied to maintain an experiment-wise error rate of  $\alpha = 0.05$ .

For each size class, we analyzed the frequency of repairs among sites and seasons using a 2-way ANOVA design. This design was also used to analyze the frequency of repairs among sites and years. Tukey multiple comparisons tests were performed where appropriate. We found heterogeneity of variances in the frequency of repairs per snail for all size classes of snails, and transformation did not correct this problem. Sample sizes were relatively large and the numbers of repairs per snail were normally distributed. Nevertheless, these results should be interpreted with caution. A  $\log(Y + 1)$  transformation corrected the heterogeneity of variances present in the comparison among sites and years.

**Predator abundance and size.** We estimated the abundance of *Callinectes* by placing crab traps at each site. Commercial traps ( $60 \times 60 \times 45$  cm) were covered in 0.5 cm Vexar mesh. Cable ties fitted across the trap openings permitted crabs  $\geq 15$  mm carapace width to enter the traps but not to escape. All traps were baited with chicken. At APM1 and PAP1, a trap was placed within the band of *Spartina* bordering open water and a trap was placed at the center of the experimental plot at APM2. At PAP2, the band of *Spartina* bordering the creek was very narrow and it was not possible to place a trap within the vegetation. Access to predators is potentially limited by travel time from the primary channel and complete drainage of the site during low tide. A trap was set at the mouth of the creek, which is the nearest aquatic point of entry, to quantify the potential number of crabs entering the creek during periods of inundation. A single trap was deployed simultaneously at each site upon retrieval of each tethering trial, and each trap was collected after 24 h. Traps were occasionally lost during storms or damaged by crabs. Data for those trapping periods in which

traps were lost or damaged at one or more sites were not included in the analysis of crab abundance and size. Four traps were deployed at each site during each season.

The carapace width of each trapped crab was measured as the distance between the bases of the lateral spines. Crabs of carapace width  $< 30$  mm were removed from the analysis because they were not capable of damaging snails in the size range used in the tethering experiments (Hamilton 1976, Schindler et al. 1994). Mud crabs were occasionally captured in the traps and enumerated. The data derived from each 24 h trap deployment consisted of mean number and size of crabs  $> 30$  mm. Crab abundance and size were analyzed using the same 3-way ANOVA design that was used to analyze the tethering results. Tukey multiple comparisons tests were employed as appropriate. Transformations were unnecessary for crab abundance and size.

**Apertural lip thickness.** We measured the apertural lip thicknesses of snails in the large size class collected for assessments of repair (sample sizes were 30 to 50 snails per site per season) to determine if trends in shell defense corresponded to among-site differences in the activity of predators. In addition, we measured the apertural lips of 50 snails collected from each of the study sites in October of 2001 and compared them to snails collected in October of 2003 to determine if among-site differences were consistent between years. Lip thickness was measured using digital calipers at the outermost flare of the aperture, the site on the shell at which crabs most often apply force to crush or peel the aperture (Hamilton 1976, Schindler et al. 1994). The data were analyzed by a 2-way analysis of covariance (ANCOVA) design, with site and season as fixed factors and shell height as a covariate. Differences among sites and years were also compared with a 2-way ANCOVA design, with site and year as fixed factors. Tukey multiple comparisons tests were performed as appropriate. Transformations were unnecessary.

***Spartina* and *Littoraria* densities.** Densities of *Spartina* and *Littoraria* were measured using a  $0.5 \text{ m}^2$  quadrat to determine if (1) dense stands of *Spartina* imposed a filtering effect on *Callinectes*, and (2) the predation pressure imposed on *Littoraria* by *Callinectes* was density-dependent. Each season, 5 random quadrats were sampled at each site (10 samples were collected from PAP1 each season due to low snail densities). Mean densities of *Spartina*, *Littoraria*, and *Callinectes* (from the crab traps) were pooled within seasons at each site and compared pair-wise by Pearson correlations. Transformations were applied as necessary to meet the assumptions of parametric statistics.

We pooled *Spartina* and *Littoraria* densities across seasons and compared them among sites to determine

if variations in density were comparable to those in continuous marshes. *Spartina* densities were compared using a 1-way ANOVA design. The variances associated with *Littoraria* densities were heterogeneous and could not be corrected by transformation. The *Littoraria* densities were compared using a Kruskal-Wallis test. Multiple comparisons tests were performed using Dunn's method.

## RESULTS

### Predation potential

Lethal attacks differed significantly among sites ( $F = 5.35$ ;  $df = 3, 42$ ;  $p = 0.003$ ) but not seasons ( $F = 2.00$ ;  $df = 2, 42$ ;  $p = 0.147$ ; Fig. 2A). The highest mean proportion of lethal attacks occurred at PAP1, and the lowest at APM2. Lethal attacks at PAP2 and APM1 did not significantly differ from either PAP1 or APM2; however, the difference in the proportion of lethal attacks at PAP1 and APM1 was marginally non-significant ( $p = 0.088$ ; Tukey multiple comparisons test). No interactions were detected between site and season for this or any other assessment class. The day on which each tethering trial was conducted was nested within seasons; day was significant ( $p < 0.05$ ) for all assessment classes.

Sublethal attacks differed among sites ( $F = 3.48$ ;  $df = 2, 42$ ;  $p = 0.024$ ) and seasons ( $F = 3.50$ ;  $df = 2, 42$ ;  $p = 0.039$ ; Fig. 2B). Differences among PAP1, APM1, and PAP2 were not distinguishable but these sites all exhibited significantly higher rates of sublethal damage than APM2. The highest proportion of sublethal damage was inflicted during the summer.

Predator-specific damage to the tethering lines differed significantly among sites ( $F = 11.68$ ;  $df = 3, 42$ ;  $p < 0.001$ ) but not seasons ( $F = 0.59$ ;  $df = 2, 42$ ;  $p = 0.560$ ; Fig. 2C). Predator-specific line damage was lowest at APM2 and indistinguishable among PAP2, PAP1, and APM1. PAP2 and APM1 did exhibit marginally non-significant differences in line damage ( $p = 0.08$ ; Tukey multiple comparisons test).

The total number of predation events differed significantly among sites ( $F = 17.96$ ;  $df = 3, 42$ ;  $p < 0.001$ ) but not seasons ( $F = 1.71$ ;  $df = 2, 42$ ;  $p = 0.193$ ; Fig. 3). Snails tethered at PAP1 and PAP2 experienced the greatest predation potential, whereas those tethered at APM2 experienced the least. Predation events at APM1 were indistinguishable from those at PAP2, but were intermediate between those at PAP1 and APM2. The cage controls showed that predators were indeed responsible for the inferred attacks on tethered snails: no damage equivalent to predation events was observed among caged controls.

### Test for statistical independence among tethering trials

The tethering trials were statistically independent in the sense that different crabs were responsible for attacks in the different trials. Of 71 crabs that were marked or tagged during the 6 wk mark-recapture study in 2002, only 2 were recaptured at APM1 1 wk after being marked and released.

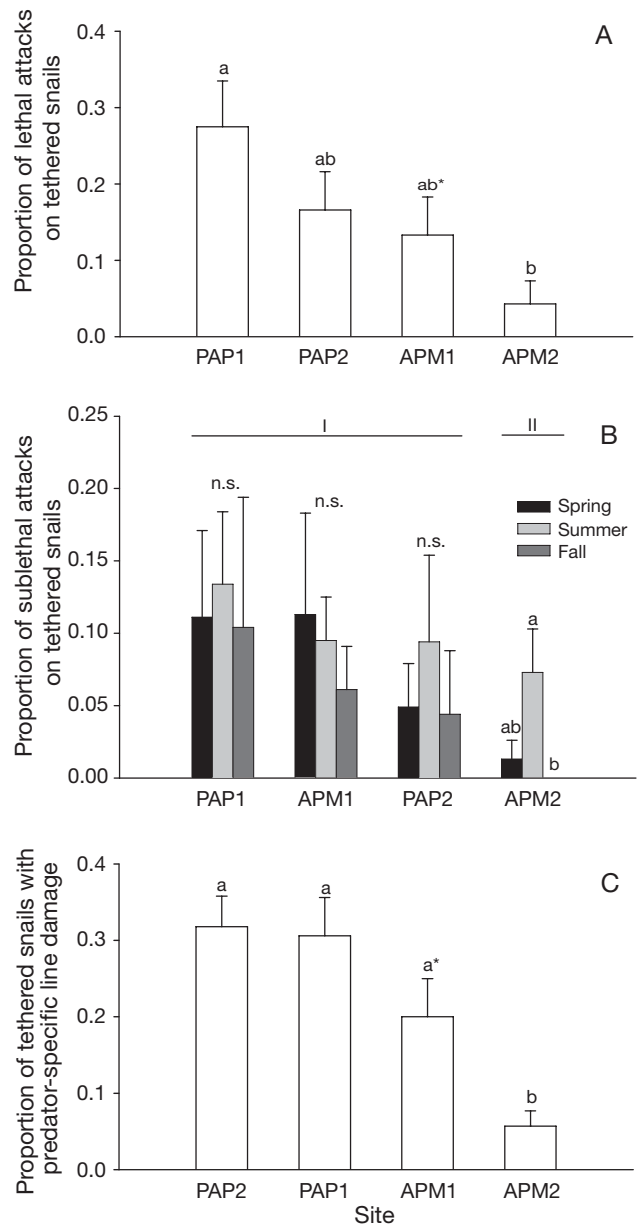


Fig. 2. *Littoraria irrorata*. Mean proportions of (A) lethal attacks, (B) sublethal attacks, and (C) predator-specific line damage. Error bars:  $\pm 1$  SE. Means with the same letter or grouped under the same numbered bar are not significantly different ( $p > 0.05$ ). Bars marked \* are marginally non-significant [(A):  $p < 0.088$  for PAP1 and APM1; (C):  $p = 0.080$  for PAP2 and APM1]

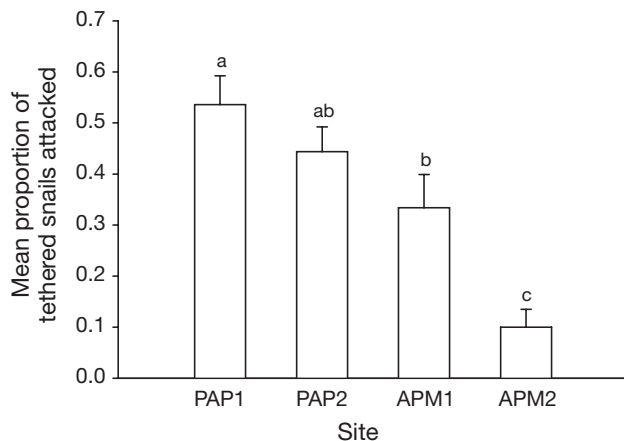


Fig. 3. *Littoraria irrorata*. Mean proportion of tethered snails attacked at each site. Error bars:  $\pm 1$  SE. Means with the same letter are not significantly different ( $p > 0.05$ )

### Sublethal damage

The number of repaired shell cracks was Poisson-distributed within all pair-wise combinations of size classes, sites and seasons, as well as sites and years ( $\alpha_{\text{adj}} = 0.05/41$  tests = 0.0012; see Table 1 for a summary of p-values). A  $4 \times 3 \times 2$   $\chi^2$  contingency-table design (site  $\times$  season  $\times$  repair presence/absence) was applied to each size class of snails ( $\alpha_{\text{adj}} = 0.05/16$  tests = 0.0031). Mutual tests of independence among sites, seasons, and repair states were significant for all 3 size classes ( $p < 0.001$ , all tests). Repair state was dependent on sites ( $p < 0.001$ ) and independent of seasons ( $p = 0.831$ ) for large snails. Repair frequencies in large snails were pooled within seasons among sites for analysis by  $2 \times 2$  contingency tables (see below). Repair state was dependent on both site and season for medium and small snails ( $p < 0.001$ , all tests). This heterogeneity between site and season precluded comparisons of sites among seasons.

A test of mutual independence among sites, years and repair states was significant ( $p < 0.001$ ) with site dependent on repair state and year ( $p < 0.001$ ), but year was not dependent on repair state or site ( $p = 0.0083$ ). A comparison of years via  $2 \times 2$  contingency tables revealed no significant difference among years (range of p-values: 0.194 to 0.764), and the high p-value can be attributed to year-to-year variability among sites (i.e. the significant dependence of repair state on site and/or year). Repair frequencies were therefore pooled within years among sites for analysis by  $2 \times 2$  contingency tables.

Within all size classes, differences among sites were analyzed separately within seasons via  $2 \times 2$  contingency tables ( $\alpha_{\text{adj}} = 0.05/41$  tests = 0.0012). Among large snails, the proportion of repaired snails was

Table 1. *Littoraria irrorata*. Summary of p-values from all  $\chi^2$  goodness-of-fit tests conducted to determine whether numbers of repaired shell cracks are Poisson-distributed;  $\alpha_{\text{adj}} = 0.05/41$  tests = 0.0012

p-value range	Number of cases
0.05 > p > 0.025	1
0.10 > p > 0.05	1
0.25 > p > 0.10	7
0.50 > p > 0.25	3
0.75 > p > 0.50	6
p > 0.75	23

greatest at PAP1 and lowest at APM2 (Fig. 4A). Levels of repair were intermediate at PAP2 and APM1. Repair also differed significantly among sites when calculated as the frequency of repair at each site ( $F = 59.66$ ;  $df = 3$ , 581;  $p < 0.001$ ; Fig. 4B). Repair was again greatest at PAP1 and lowest at APM2. As before, PAP2 and APM1 exhibited intermediate levels of repair, but PAP2 exhibited significantly greater levels of repair than APM1. No seasonal effects were detected. The heterogeneity of variances in numbers of repairs per snail is attributed primarily to the low number of repairs at APM2.

Among medium- and small-sized snails, significant differences in proportions of repair were detected among sites in both spring and summer, but not during fall (Fig. 5). PAP1 exhibited the highest proportion of repair in both size classes during spring and summer, with no detectable differences among PAP2, APM1, and APM2. Similarly, frequencies of repair for both medium and small snails were highest at PAP1, with no detectable differences among PAP2, APM1, and APM2 (ANOVA results for differences among sites; medium snails:  $F = 15.35$ ;  $df = 3$ , 507;  $p < 0.001$ ; Fig. 6A; small snails:  $F = 13.84$ ;  $df = 2$ , 419;  $p < 0.001$ ; Fig. 6B). No seasonal differences were detected among medium snails, and frequencies were pooled within seasons among sites. Small snails at PAP1 exhibited significantly higher frequencies of repair per snail than those at PAP2 and APM1 during spring and summer, but not in fall.

Small snails collected in spring exhibited significantly higher frequencies of repair than those collected in summer or fall ( $F = 10.93$ ;  $df = 2$ ;  $p < 0.001$ ). A significant site  $\times$  season interaction was detected for the frequency of repair per snail in small snails ( $F = 3.36$ ;  $df = 4$ ;  $p = 0.01$ ). This interaction is attributed to the significant differences among sites within spring and summer but not during fall.

For large snails, proportions of repair compared among sites and pooled across years were greatest at PAP1, lowest at APM2, and intermediate at PAP2 and APM1 (Fig. 7A). Calculated as the frequency of repair, a significant difference was detected among



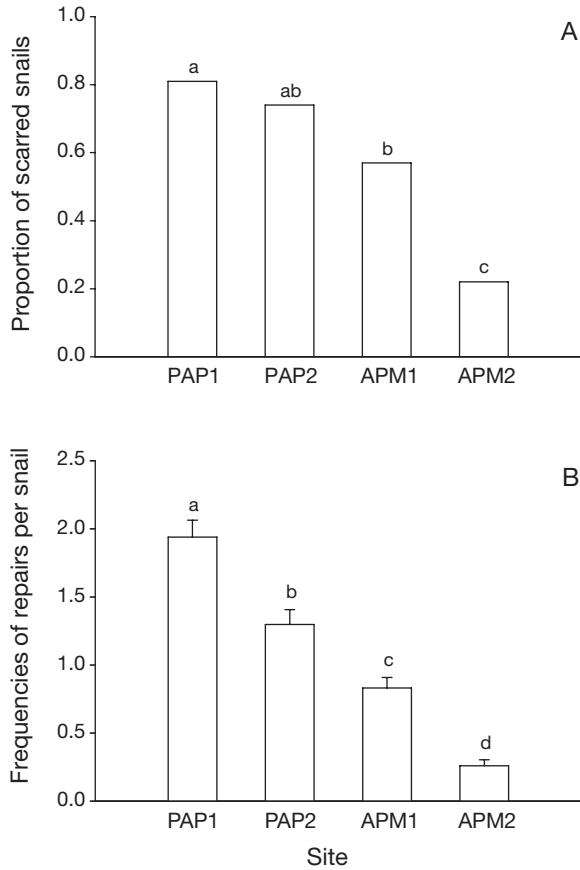


Fig. 4. *Littoraria irrorata*. Repairs in large snails ( $\geq 17$  mm shell length) collected in 2003 and compared among sites: (A) proportion of snails with  $\geq 1$  sublethal injury and (B) mean number of repairs per snail. No significant differences were detected among seasons; data for both (A) and (B) were pooled within seasons, and means for each site presented. Error bars:  $\pm 1$  SE. Means with the same letter are not significantly different ( $p > 0.05$ )

sites ( $F = 66.35$ ;  $df = 3, 588$ ;  $p < 0.001$ ; Fig. 7B) but not among years ( $F = 1.64$ ;  $df = 3, 588$ ;  $p = 0.196$ ). Repair was greatest at PAP1, lowest at APM2, and intermediate at PAP2 and APM1. PAP2 exhibited significantly greater levels of repair than APM1. Although there were no overall differences in repair among years, a significant site  $\times$  year interaction was detected ( $F = 8.61$ ;  $df = 6, 588$ ;  $p < 0.001$ ) and is attributed to the high levels of repair at APM1 in 2001 and PAP2 in 2003. No significant differences were detected among years at PAP1 or APM2.

#### Predator abundance and size

Crab abundance varied significantly among sites and seasons (log-transformed data, site:  $F = 11.65$ ;  $df = 3, 27$ ;  $p < 0.001$ ; season:  $F = 6.12$ ;  $df = 2, 27$ ;  $p = 0.006$ ;

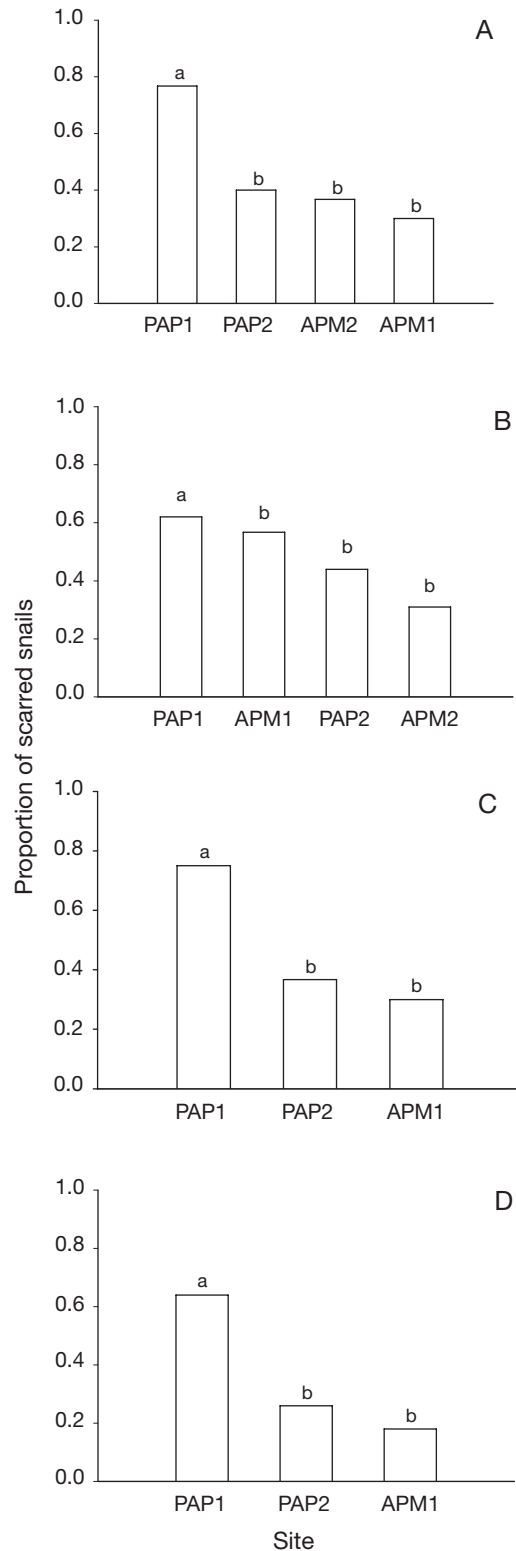


Fig. 5. *Littoraria irrorata*. Repairs in medium and small snails expressed as proportion of snails with  $\geq 1$  sublethal injury: (A) medium snails in spring, (B) medium snails in summer, (C) small snails in spring, (D) small snails in summer. Means with the same letter are not significantly different ( $p > 0.05$ )

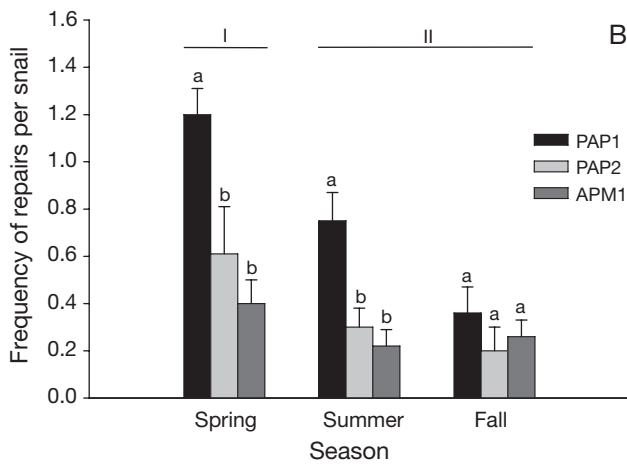
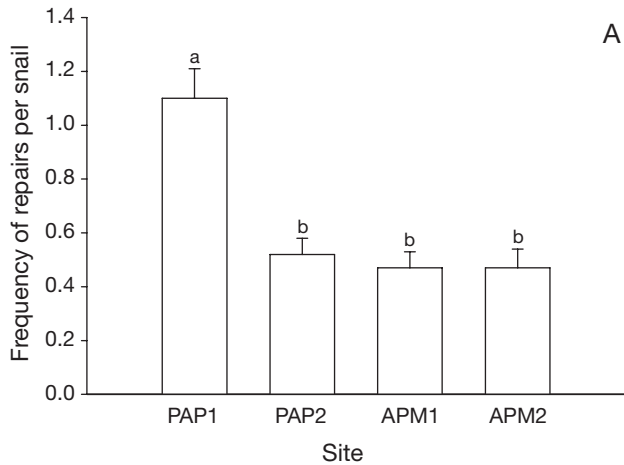


Fig. 6. *Littoraria irrorata*. Repairs in (A) medium and (B) small snails expressed as frequency of repairs per snail. No significant differences were detected among seasons for medium snails; data were pooled within seasons, and means for each site presented. Means with the same letter and sites grouped under the same numbered bar are not significantly different ( $p > 0.05$ )

Fig. 8A). Crabs were most abundant at PAP1, and no significant differences were detected among APM2, PAP2 or APM1. Crab abundance was greatest during summer, intermediate in fall, and lowest in spring. No seasonal differences were detected within sites. Only 5 mud crabs were caught during the course of the study: 2 each at APM1 and APM2, and 1 at PAP2.

Mean carapace width of crabs caught in the traps differed significantly among sites and seasons (site:  $F = 27.04$ ;  $df = 3, 27$ ;  $p < 0.001$ ; season:  $F = 4.94$ ;  $df = 2, 27$ ;  $p = 0.015$ ; Fig. 8B). A significant interaction between sites and seasons ( $F = 2.81$ ;  $df = 6, 27$ ;  $p = 0.029$ ) resulted from significant within-site seasonal differences at APM1 but not at PAP1, PAP2, or APM2. Crab size did not differ among APM1, PAP1, or PAP2; however, mean carapace width at these 3 sites was

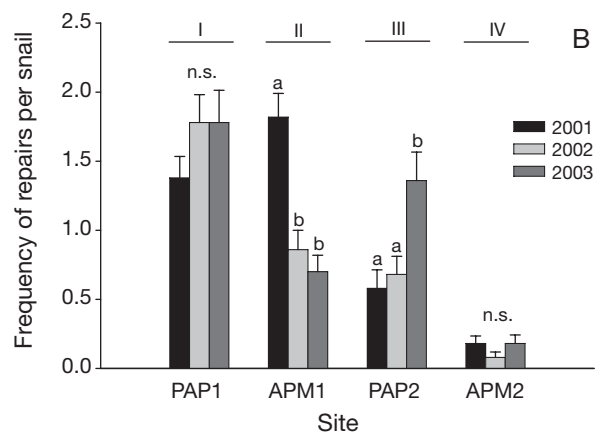
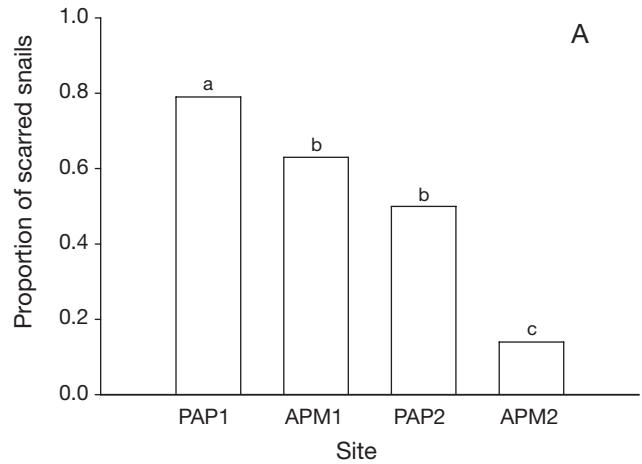


Fig. 7. *Littoraria irrorata*. Repairs in large snails ( $\geq 17$  mm shell length) compared among sites and years: (A) proportion of snails with  $\geq 1$  sublethal injury and (B) frequency of repairs per snail. No significant differences in mean number of repairs per snail were detected among seasons; data were pooled within years, and means for each site presented. Error bars:  $\pm 1$  SE. Means with the same letter or grouped under the same numbered bar are not significantly different ( $p > 0.05$ )

greater than that at APM2. APM1 was the only site for which within-site seasonal effects were detected (1-way ANOVA,  $F = 5.50$ ;  $df = 2, 9$ ;  $p = 0.028$ ). Crabs caught at APM1 were largest in fall, smallest in summer, and intermediate in spring.

### Apertural lip thickness

Apertural lip thickness varied significantly among both sites and seasons (site:  $F = 67.62$ ;  $df = 3, 487$ ;  $p < 0.001$ ; season:  $F = 17.95$ ;  $df = 2, 487$ ;  $p < 0.001$ ; Fig. 9A), and shell height was a significant covariate for lip thickness ( $F = 34.65$ ;  $df = 1, 487$ ;  $p < 0.001$ ). Mean lip thicknesses presented in Fig. 9 are covariate-

adjusted means calculated using Minitab 14.2. Lip thickness differed significantly among all 4 sites: snails at PAP1 exhibited the thickest apertural lips, and those at APM2 exhibited the thinnest lips. A significant interaction between site and season ( $F = 4.50$ ;  $df = 6, 487$ ;  $p < 0.001$ ) resulted from large seasonal differences at PAP1 and PAP2 but not at APM1 or APM2. Lip thickness was greatest during spring at PAP1 and PAP2, with no detectable differences between summer and fall.

Lip thickness also varied significantly among sites and years (site:  $F = 41.97$ ;  $df = 3, 374$ ;  $p < 0.001$ ; year:  $F = 19.27$ ;  $df = 1, 374$ ;  $p < 0.001$ ; Fig. 9B), and shell height was a significant covariate for lip thickness ( $F = 25.15$ ;  $df = 1, 374$ ;  $p < 0.001$ ). Apertural lips were thickest at PAP1, intermediate at PAP2 and APM1, and thinnest at APM2. Snails collected in 2001 exhibited

significantly thicker lips than those collected in 2003 (apertural lip thickness  $\pm$  SE, 2001:  $1.65 \pm 0.01$  mm; 2003:  $1.58 \pm 0.01$  mm).

### *Spartina* and *Littoraria* densities

There was a significant positive correlation between mean *Littoraria* and *Spartina* densities (log-transformed counts;  $n = 12$ ;  $r = 0.65$ ;  $p = 0.024$ ; Fig. 10A). Mean crab abundance was negatively correlated with both *Spartina* density (square root-transformed data;  $n = 12$ ;  $r = -0.61$ ;  $p = 0.031$ ) and mean snail density (square root-transformed data;  $n = 12$ ;  $r = -0.72$ ;  $p = 0.008$ ). A significant negative relationship between crab and snail abundance was still detected after snail

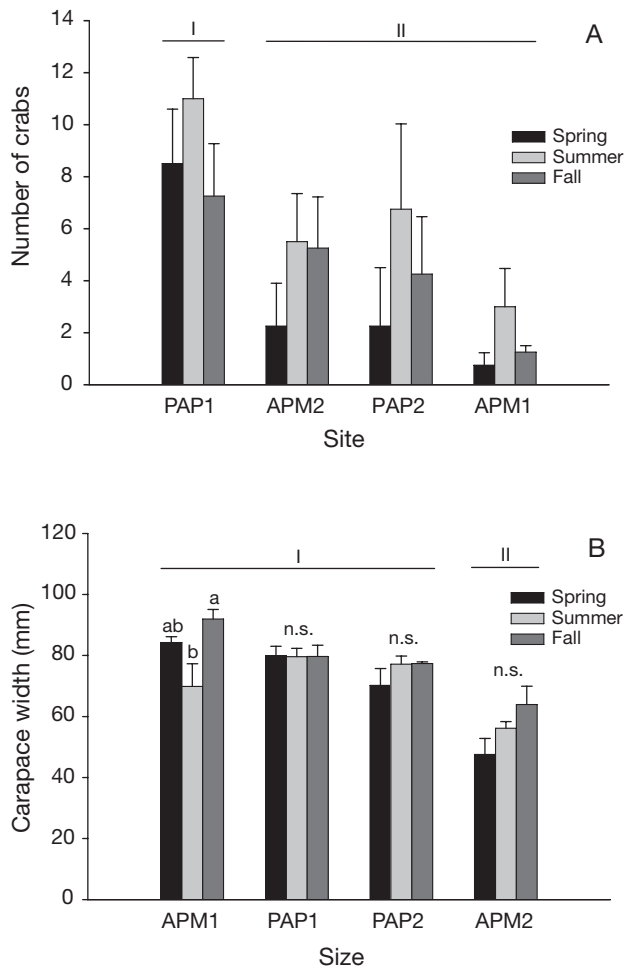


Fig. 8. *Callinectes sapidus*. (A) Abundance and (B) carapace width of crabs compared among sites and seasons. Error bars:  $\pm 1$  SE. Sites grouped under the same numbered bar are not significantly different ( $p > 0.05$ ). See 'Results' for seasonal differences in crab abundance among sites. No within-site seasonal effects were detected for crab abundance or size

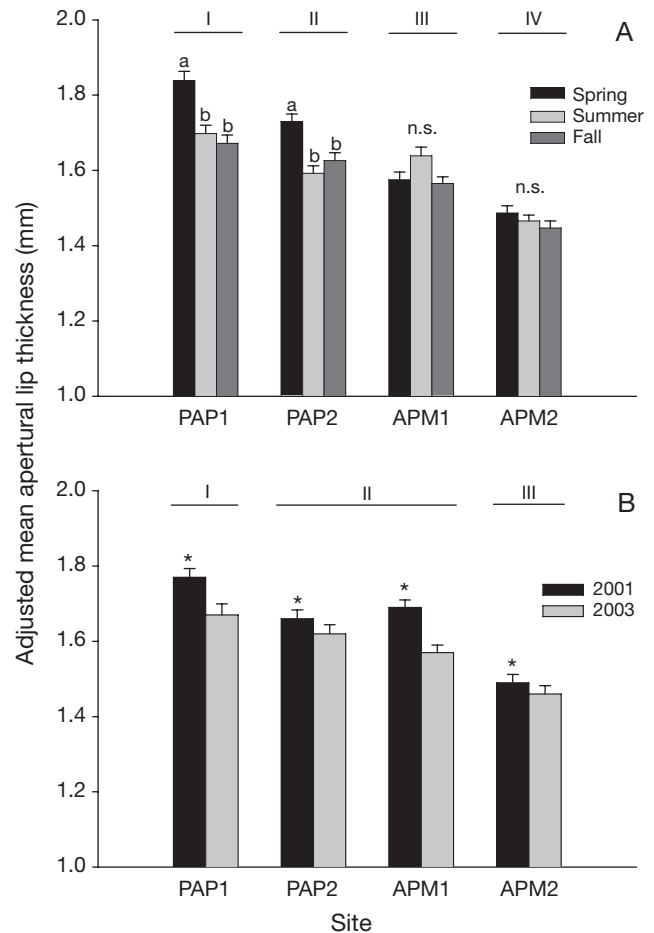


Fig. 9. *Littoraria irrorata*. (A) Comparison of apertural lip thicknesses among sites and seasons of large snails ( $\geq 17$  mm shell length) in 2003 and (B) apertural lip thicknesses of large snails in fall 2001 and 2003. Error bars:  $\pm 1$  SE. Sites grouped under the same numbered bar are not significantly different ( $p > 0.05$ ); within each site, seasons with the same letter in (A) are not significantly different ( $p > 0.05$ )

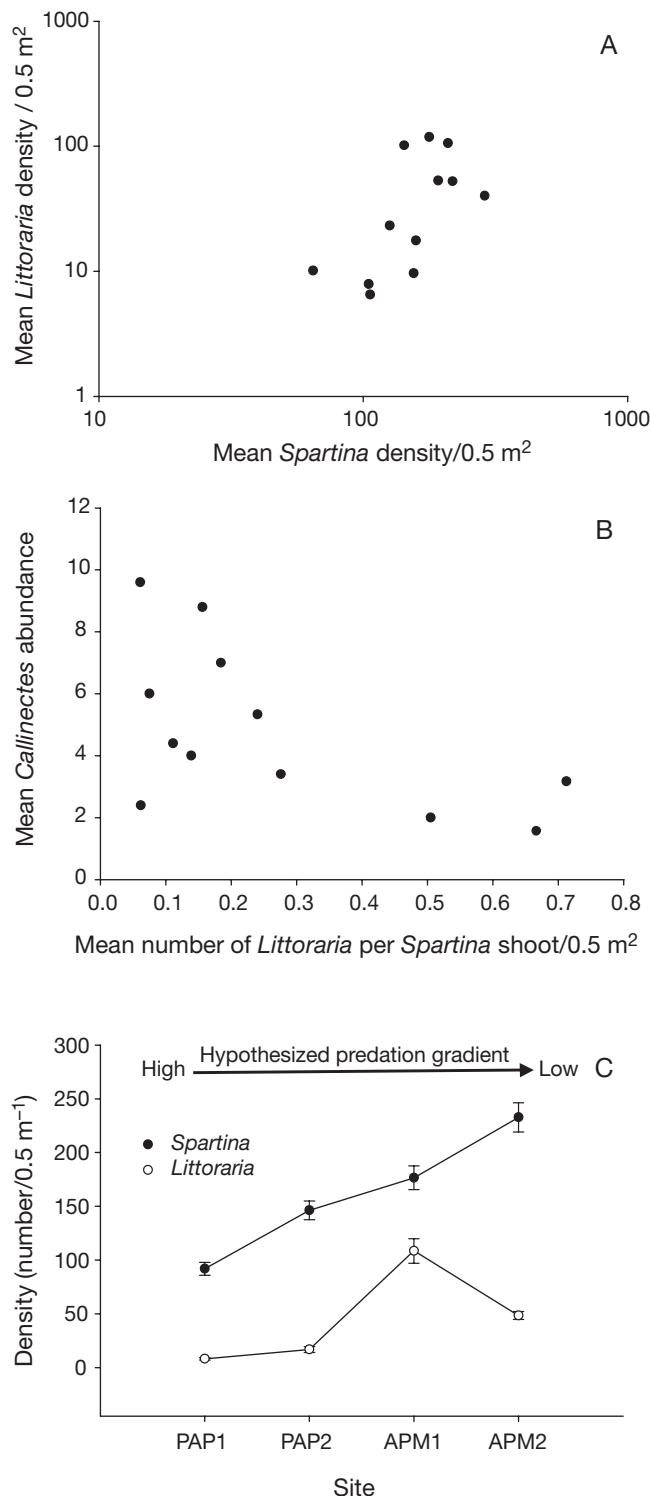


Fig. 10. Logarithmic relationship between (A) mean *Littoraria* and *Spartina* densities, (B) mean *Callinectes* abundances and mean density of *Littoraria* standardized for *Spartina* density (see 'Results' for calculations), and (C) *Spartina* and *Littoraria* densities at each study site. Sites in (C) ordered along our hypothesized predation gradient; the 12 data points in (A) and (B) are pooled values of data from 4 sites collected over 3 seasons. Error bars:  $\pm 1$  SE

densities were standardized across sites by dividing mean snail densities by the respective *Spartina* densities (untransformed data;  $n = 12$ ;  $r = -0.61$ ;  $p = 0.036$ ; Fig. 10B).

*Spartina* and *Littoraria* densities varied significantly among sites (*Spartina*:  $F = 45.59$ ;  $df = 3, 71$ ;  $p < 0.001$ ; *Littoraria*:  $H = 55.40$ ;  $df = 3$ ;  $p < 0.001$ ; Fig. 10C). APM2 exhibited the densest stand of *Spartina* and PAP1 exhibited the sparsest. *Littoraria* was densest at APM1 and APM2, and lowest at PAP2 and PAP1. *Littoraria* densities did not significantly differ within marshes.

## DISCUSSION

We detected a strong positive relationship between predation potential, sublethal predation, predator abundance, and architectural defense in *Littoraria* shells among sites (i.e. among subhabitats) that varied in their accessibility to *Callinectes*. Furthermore, the sites varied in inundation time and, consequently, the number of hours that crabs had access to prey each day. Despite the disjunct nature of the study sites, these small-scale spatial variations in predation are not only distinct but appear to persist over relatively long periods of time (i.e. over multiple years). In addition, the distributions of sublethal repairs in *Littoraria* shells indicate that attacks by *Callinectes* are randomly inflicted on *Littoraria* irrespective of attack frequency. Taken together, these results suggest that variations in both flooding regime and physical structure maintain distinct, heterogeneous predation regimes across disjunct *Spartina* patches.

In agreement with previous studies, the degree to which *Callinectes* had access to prey within the marsh was dictated primarily by *Spartina* density, surface elevation, and isolation from open water. PAP1, located directly on the shore of Mississippi Sound, exhibited the lowest *Spartina* densities, remained inundated throughout most of the study, and exhibited the highest levels of predation by all measures. In contrast, the lowest predation levels were found at APM2, a densely vegetated area located in the high-marsh zone.

## Predation potential

Although the tethering experiments enhanced the availability of *Littoraria* to *Callinectes* and exaggerated natural rates of attack, the relative differences in predation potential among sites mirrored patterns of shell repair for large snails. This result bears out Vermeij's (1982) suggestion that sublethal injuries reflect natural rates of predation pressure on gastropod populations. Lethal attacks on tethered snails and predator-

specific line damage on tethered snails produced the same groupings of subhabitats as did the pooled analysis of total predation events. This result strongly supports *Callinectes* as the primary shell-crushing predator within our study marshes.

The occurrence of sublethal attacks on tethered snails was highly variable and did not account for a large proportion of the total number of attacks on tethered snails. This is not surprising, given the low frequencies observed in our repair assessments (which reflect natural predation rates); snails at PAP1, the site of highest *Callinectes* activity, incurred an average of only 2 scars per lifetime, even though individual snails had as many as 7 scars. Despite possible lethal and sublethal attacks by mud crabs and birds on tethered snails at APM2 and, to a lesser extent, APM1 and PAP2, the data show a clear trend of high predation rates at PAP1, low predation rates at APM2, and intermediate rates at APM1 and PAP2.

### Predator abundance and size

Variances of crab abundance were high within sites, resulting from few trap deployments throughout the course of the study and natural variations in crab activity among tidal cycles. Furthermore, the use of baited traps most likely enhanced estimates of crab numbers by attracting crabs over a relatively large area at each site. However, we were able to discern that crabs were most abundant during summer, and this seasonality was also reflected in the number of sublethal attacks on tethered snails. Crab abundances were lowest during spring, a known period of crab recruitment (Rabalais et al. 1995, Heck et al. 2001), and the high frequency of repair for all size classes of snails at PAP1 and PAP2 during this period likely reflects an influx of juvenile crabs during this period. *Callinectes* <30 mm in carapace width were excluded from our analysis, but they are more than capable of damaging and consuming snails of 5.00–11.99 mm shell length (Hamilton 1976, Schindler et al. 1994).

### Sublethal repair

Sublethal repairs were randomly distributed across all size classes of *Littoraria*. In other words, a snail with one or more repairs was not disposed to either more or fewer future repairs. The random nature of unsuccessful attacks was consistent with the tactile foraging methods used by *Callinectes* in the turbid and densely vegetated waters of Mississippi Sound and surrounding coastal areas. These results suggest that snails do not alter their behavioral patterns while repairing

damage to the shell (e.g. they do not seek refuge or exhibit an enhanced escape response during this time), nor is a recently repaired shell more prone to future damage relative to undamaged shells. However, it remains unclear whether the occurrence of sublethal damage is correlated with lethal attacks.

When sublethal damage was expressed as the frequency of repairs per individual, we were able to resolve differences among sites more precisely than when repair was expressed as the proportion of repaired snails. However, both methods provided sufficient separation among sites, and the congruence of the 2 metrics of shell repair resulted from the random distribution of individual injuries within the snail populations. Sublethal damage by either method of calculation provides an accurate relative measure of predation pressure in populations of prey confronted with the same predator or suite of predators.

The shells of large snails provided a stable, time-integrated record of predation, whereas only extremes in predation intensity were discernible among small and medium size classes of snails. Relative differences in repair among large snails were constant over both seasonal and annual scales, a consequence of random attacks by predators and, more importantly, the relatively old age of this size class; growth rate estimates by Stiven & Hunter (1976) indicate that the size class defined as 'large' in this study exceed 7 yr of age. The proportions of scarred snails of  $\geq 17$  mm shell length assessed in this study agree closely with those of previous studies from the Atlantic coast (Table 2). However, significant seasonal variations in repair were detected among small snails, with the highest levels of predation occurring in spring. These results are consistent with high frequencies of repair observed in juvenile *Littoraria* during spring by Warren (1985) and the presence of *Callinectes* recruits. The lack of resolution among sites in the small and medium size classes likely resulted from rapid growth in young snails, seasonal variability in the activity of predators, and the susceptibility of juveniles to predation by small predators capable of entering structurally-complex habitats. Records of shell repair taken from assemblages of juveniles alone could underestimate overall predation intensity, yet still serve to elucidate small-scale ecological patterns.

Low frequencies of sublethal damage can be problematic because they can result from either low or very high frequencies of lethal encounters (Schoener 1979, Medel et al. 1988, Leighton 2002). However, in long-lived species, older age-classes inhabiting environments restrictive to predators are unlikely to exhibit a complete absence of repair if predators pose at least some threat to the population. Conversely, a population that persists under very high levels of predation intensity will necessarily accumulate a greater propor-

Table 2. *Littoraria irrorata*. Comparison of repair frequencies in large snails ( $\geq 17$  mm shell length) from the Atlantic and Gulf Coasts

Location	Proportion (low marsh $\rightarrow$ high marsh)	Source
Coastal Alabama	0.81 to 0.22	This study
Sapelo Island, Georgia	0.67 to 0.20	Schindler et al. (1994)
Wallops Island, Virginia	0.60 (low marsh only)	Stanhope et al. (1982)

tion of repair relative to populations under low predation intensity if the same suite of predators randomly attacks individuals in both populations. If repairs are randomly distributed in a population, then predator identity should be more important than predator abundance in determining whether measures of repair are comparable among populations. The difficulty associated with interpreting very low instances of repair in randomly attacked populations is ultimately an issue of undersampling (i.e. a small sample size results in a collection of undamaged individuals) rather than an artifact of very low or very high predation intensity.

#### Apertural lip thickness

Variations in lip thickness differed among sites in the same pattern as measures of predation potential and sublethal repair, and remained stable at both seasonal and annual scales. Overall, snails collected in 2001 exhibited greater lip thickness than those collected in 2003. This difference could be due to interannual differences in predator activity, or to variable calcification rates resulting from interannual variations in food availability, salinity, and water temperature. Lip thickness at PAP1 and PAP2 was highest during spring, contemporaneous with the spring recruitment of crabs, but seasonal differences were not detected at APM1 and APM2. Assuming that the abundances of recruits (which were not quantified in this study) vary in a manner similar to those of larger crabs, and given the differences in crab activity among these sites, the water-borne cues produced by a large number of small crabs could generate this pattern even though crab recruits are unable to consume the size range of snails measured ( $\geq 17$  mm shell length). This assumes that morphological responses are dose-dependent and that snails are unable to differentiate (e.g. chemically or visually) among the sizes of predators in the marsh.

Greenfield et al. (2002) found that *Littoraria* inhabiting an area regularly accessible to *Callinectes* expressed thicker apertural lips relative to individuals inhabiting the high marsh, and provided evidence for the role of past predation in enhancing shell defenses. Blundon & Vermeij (1983) demonstrated that sublethal

repairs do not significantly weaken the shell of *Littoraria*. Together these studies show that *Littoraria* is capable of rebuilding the aperture to pre-attack strength, if not to a greater extent. Our study strengthens the relationship between crab accessibility and apertural lip thickness, but further research is necessary to distinguish whether morphological differences in *Littoraria* arise from selective predation, the

occurrence of past experiences with predators, or induction by water-borne predatory cues (which has been demonstrated in the littorinid *Littorina obtusata*; Trussell 1996). Laboratory and field data suggest that water-borne cues are the primary mechanism driving differences in shell architecture in *Littoraria irrorata* (R. Moody unpubl. data).

#### *Littoraria* and *Spartina* densities

*Littoraria* and *Spartina* densities were positively correlated; however, this relationship was weakened somewhat by high densities of juvenile *Littoraria* at APM1. The abundance of *Callinectes* was negatively correlated with *Spartina* density, *Littoraria* density, and *Littoraria* density expressed as the average number of snails per *Spartina* shoot. Encounter rates between *Callinectes* and *Littoraria* are, therefore, negatively density-dependent. These findings agree with Lewis & Eby's (2002) finding that *Spartina* imposes a filtering effect on the size and number of crabs able to enter interior vegetation zones. Furthermore, the negative relationship between *Callinectes* abundance and standardized *Littoraria* density reflects an additional filtering effect on crab abundance associated with a seaward-to-landward trend of increasing elevation.

In addition to among-site differences in density, *Spartina* was present in different growth forms at each site, affecting the availability of refuges for snails at each site. Tethered snails were not permitted to climb, which could have overestimated predation intensity at sites with taller *Spartina* growth forms relative to sites with shorter growth forms (i.e. snails might have climbed higher on taller grass). However, assessments of sublethal repair and shell architecture integrated the effects of grass height, and the among-site differences observed in these metrics were identical to those observed in the tethering experiments.

#### Implications and applications

Spatial heterogeneity is vital to the maintenance of diversity, function, and stability and persistence of

prey populations in many systems (e.g. Menge 1976, Minello & Zimmerman 1983, DeAngelis & Waterhouse 1987, Kareiva 1987). This is especially true for salt marshes, including those in the northern Gulf of Mexico, which are highly productive ecosystems that provide food, refuge, and nursery habitat for commercially important fish and crustaceans (Rountree & Able 1993, Peterson & Turner 1994, Kneib 1997, Minello & Webb 1997). Within our study area, disjunct patchworks of *Spartina* stands in the northern Gulf of Mexico exemplify the range of heterogeneous subhabitats present within the continuous marshes that characterize the Atlantic Coast and Mississippi River delta regions. Distinct among-site variations in the predatory activities of an abundant and important aquatic predator, *Callinectes*, are established and maintained over very small scales (10s to 100s of meters) and persist over multiple years. This reflects the persistence of subhabitats in these marshes, and the benefits—refuges in particular—that they confer to potential prey species that utilize them.

Given the maintenance of predation regimes on a fine spatial scale and the random foraging behavior of *Callinectes* on *Littoraria*, assessments of sublethal repair and shell architecture in *Littoraria* could serve as accurate ecological proxies for the predatory activities of *Callinectes* within *Spartina*-dominated marshes. When prey are randomly sampled by their predators, both tethering experiments and assessments of sublethal repair integrate the abundance and activity of predators, variations in structural heterogeneity of the habitat, and other aspects of predation pressure. For example, Silliman & Bertness (2002) found that *Littoraria* has the potential to graze down *Spartina* marshes in the absence of predation by *Callinectes*. Using the proxies derived in this study, it might be possible to identify marshes that are at risk.

The results of this study are particularly germane to habitats in which *Callinectes* is the primary shell-crushing predator, but similar metrics could be derived for other predator-prey systems if the primary shell-crushing predators were known. The strength of *Littoraria*-*Callinectes* interaction could be particularly useful as a rapid and inexpensive proxy for evaluating the development of ecological function over time within created and restored salt-marsh habitats. *Spartina* is an essential structural component of salt marshes in the southeastern United States, and is one of the primary targets of coastal restoration projects. Although *Callinectes* and many of the mobile taxa that constitute its prey rapidly colonize created/restored marsh habitats, it is not clear whether or when naturalistic or quasi-naturalistic trophic relationships become established (Minello & Zimmerman 1992, Jivoff & Able 2003). Likewise, it is unclear whether or when restored

marshes provide sufficient prey resources required to support *Callinectes* populations, which are the basis of important commercial fisheries in the southeast.

Assessments of sublethal repair, shell architecture, and predation on tethered *Littoraria* potentially correlate with the intensity of predation on other resources and, by extension, with overall levels of trophic transfer to *Callinectes*. Financial and logistical constraints generally limit marsh restoration to small spatial scales of <50 ha. Our results suggest that distinct levels of structural heterogeneity and distinct trophic regimes are naturally maintained well within these spatial scales.

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